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Vegetation change in boreonemoral forest during succession — trends in species composition, richness and differentiation diversity

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We compared the diversity and composition of understorey vegetation of four successional stages (recently clearcut, young, middle-aged and old stands) in an Estonian boreonemoral coniferous forest under homogeneous soil conditions. The ordination analysis (NMDS) showed that successional age was the main driver of understorey species composition with soil pH and P content responsible for some variation as well. Species composition in old-growth stands was more similar to the vegetation of young and clear-cut stands than to the composition of mid-aged stands. Species richness in 1-m^2 plots was higher in recently disturbed and young stands due to the higher abundance of disturbance-related species. The differentiation diversity, characterising species turnover among plots within a stand, was higher in recently disturbed and young stands than in mid-aged and old stands. The results indicate that earlier successional stages are characterised by spatially heterogeneous and diverse vegetation, whereas older stands develop more homogeneous vegetation composition.

Key words: boreonemoral forest, differentiation diversity, diversity, NMDS, spatial turnover, succession

Introduction

In human-impacted landscapes, forests form a mosaic of varying successional stages, representing different regeneration stages after agricultural use, fires and logging (Vellend 2003, Verheyen *et al.* 2003). Knowledge of forest disturbance and successional processes is a prerequisite for developing ecologically sustainable forest management strategies (Kuuluvainen 2002, Kangur *et al.* 2005). In particular, clearcut logging and different means of forest management such as thinning and selective felling of trees have significant impact on the diversity and composition of plant communities. Although intensive felling methods may result in a decrease in species richness in the short term (Jalonen & Vanha-Majamaa 2001), several authors reported higher species diversity in recently clearcut areas as compared with that in old-growth stands (Zobel 1989, Zobel 1993, Reich *et al.* 2001, Haeussler *et al.* 2002, Pykälä 2004, Small & McCarthy

2005). Species richness in mid-aged managed forests in previously clearcut areas have been shown to be lower (Duffy & Meier 1992, Qian *et al*. 1997), similar (Okland *et al*. 2003) or higher (Scheller & Mladenoff 2002) than in undisturbed old-growth stands. The increase in diversity after recent clearcutting occurs mainly due to the higher abundance of disturbance-related and light-demanding species, e.g. ruderals and grassland species which will be replaced by shade-tolerant perennials and other forest interior species during later successional stages (Decocq *et al*. 2004, Pykälä 2004).

In addition to the species composition of forest plant communities, management influences the spatial structure of vegetation. The amount of coarse woody debris (CWD) may vary widely depending on the management history of the forest (Köster *et al*. 2005). CWD in old-growth stands supplies specific habitats for several species and appears to be important for the maintenance of species diversity (Siitonen 2001, Miller *et al*. 2002, Lõhmus *et al*. 2005). Old-growth stands are characterised by an inverse J-shaped age structure of the tree layer (Lorimer *et al*. 2001) and by the presence of mosaic light conditions due to canopy gaps (Attiwill 1994), which may create differences in the spatial structure of understorey vegetation. Although Haeussler and Bergeron (2004) observed no difference in beta diversity between burned and clearcut areas after some years of disturbance, Qian *et al*. (1997) showed that the within-stand dissimilarity between vegetation plots was higher in old-growth forest as compared with that in a 40-yr-old plantation. Similarly, Bobiec (1998) reported higher structural diversification in an old-growth forest compared to young forest.

Forests cover more than 51% of the total area of Estonia (Pärt *et al*. 2008), most of which are managed in order to produce timber. The intensity of forest management has increased considerably during the last decades. Previous research showed that although the vegetation composition may change during the post-logging succession, plant diversity is higher in recently disturbed stands, excluding the forests on calcareous soils (Zobel 1989, 1993). Kohv and Liira (2005) and Liira *et al*. (2007) showed that when forest stands of similar successional age are compared, local anthropogenic disturbances such as forest management and recreational activities may create differences in vegetation structure and increase diversity due to the facilitation of either light-demanding or eutrophic species. Although the distribution of several rare forest species may be associated with natural disturbances (Reier *et al*. 2005, Ilisson *et al*. 2006), there is no evidence that these species regenerate under human-induced disturbances.

A recent study on forest understorey vegetation in differently managed stands in Estonia determined that management intensity was the main driver of community composition (Moora *et al*. 2007). There were no differences in species richness between old and young stands, but in contrast to the hypothesis that heterogeneity would increase during the secondary succession and later peak in old stands, significantly higher spatial turnover of species was recorded within young planted stands. Since this study was limited to young and old stands, we wanted to see if this trend is true for the whole succession from clearcut to old stand.

In particular, we aimed to use the 'space-for-time substitution' approach (Pickett & Cadenasso 2005) and compare the vegetation composition and structure of boreonemoral forest stands representing a successional sere from recent clearcut with old growth in similar soil conditions. First, we were interested in the relative role of successional age and soil parameters in determining species richness and composition. Second, we were interested how the species richness differs in recently disturbed stands as compared with that reported in earlier studies. Third, we wanted to see whether the higher differentiation diversity (spatial turnover in species composition) in young stands, as compared with that in old stands, characterises all successional phases during the post-logging succession.

Materials and methods

Study site

Estonia is located in northern Europe on the eastern coast of the Baltic Sea and the vegetation of Estonia belongs to the boreonemoral zone (Sjörs 1965). The study site was located in Koeru, central Estonia (58°97´N, 26°05´E), an area within a flat landscape with a mosaic of cultivated arable areas and forest. The climate in the study area is transitional between maritime and continental. The mean annual precipitation is 700–750 mm and the mean annual air temperature is 4.3 °C–6.5 °C, ranging between –6.8 °C in January and 16 °C in July (Jaagus 1999).

The study site is a forest area sized about 130 ha representing a *Hepatica* site type (Lõhmus 2004). The soil represents calcaric cambisol with relatively homogeneous soil conditions throughout the study area (Zobel *et al*. 2007). Norway spruce (*Picea abies*) is the dominant tree species with individuals of *Fraxinus excelsior* and *Acer platanoides* growing in old stands, and *Betula pendula* and *Tilia cordata* in young stands. *Corylus avellana* dominates the shrub layer in old stands. There is no history of arable cultivation within the Koeru forest area. Clearcutting took place repeatedly in patches of approximately 1–2 ha, although a part of the forest can still be classified as old growth, with different age classes present and the oldest spruces being 130–140 years old.

Methods

We included four successional ages in the study design: 1 = areas that were clearcut 5 years ago. 2 = young stands were clearcut 20–25 years ago and were later planted with Norway spruce. The growing stock in young stands is about 30–60 m^3 ha, the mean height of trees 5–8 m and the mean diameter 4–8 cm. The percentage of Norway spruce varies from 70% to 90%. 3 = mid-aged stands are dominated by trees of about 70–75 years old. The growing stock is approximately 273–323 m^3 ha, the mean height is 23–28 m and the mean diameter 24–28 cm. The proportion of Norway spruce varies from 83%–95%. 4 = old-growth stands are on average about 100 years old with older trees 130–140 years old. The growing stock in old-growth stands is about 280–310 m^3 ha, the mean height of trees 28 m and diameter 28–30 cm. The percentage of Norway spruce is about 96%–97%. Young and mid-aged stands were thinned repeatedly in order to reduce tree density in general and to eliminate deciduous trees in particular. Analysing the management records dating back to the 1920s revealed that the intensity of forest management was low in old-growth stands during the last century, with only occasional selective felling of individual old trees.

We sampled the understorey vegetation in three stands in each of the four successional stages in the summer of 2005. The stands were selected randomly with a criterion of spatial homogeneity, as well as well-recorded management history for every stand. Five blocks of 10 × 10 m were randomly selected within a relatively uniform area in each homogeneous stand of about 50 × 50 m. Within these blocks, five 1-m^2 vegetation plots were examined. We visually estimated the percentage coverage of all vascular plant species. For species covering less than 1%, coverage value of 0.5% was used. For coverages in ranges of 1%–10%, 11%–20%, 21%–50%, 51%–100% the coverages were determined with precisions of 1%, 2%, 5% and 10%, respectively. Altogether, we examined 300 plots within 60 forest blocks.

In each block, we took topsoil samples (depth: 1–5 cm) from the centre of each plot and pooled the samples. Samples were sieved to remove roots and then analyzed. Soil pH_{KCl}, N, K, P, Mg and Ca contents, as well as the amount of organic matter (loss of ignition) were determined according to the method of Moore and Chapman (1986).

Data processing

Non-metric multidimensional scaling (NMDS) was used in order to analyse the variation of vegetation composition with respect to the forest age and environmental variables. NMDS is a nonparametric multivariate ordination technique well suited to ecological datasets as it does not assume a normal distribution along the environmental gradients and can accommodate data on arbitrary or discontinuous scales (McCune & Grace 2002). The method reduces the multidimensional variation of the data set to variation in two or three significant dimensions. For the ordination we used the species composition of 10 × 10-m blocks, i.e. the pooled species composition of five 1-m^2 plots within 10 × 10 m blocks. In the preliminary runs we applied Bray-Curtis distances and the following settings: the starting number of axes was 4, the number of real runs 50, the number of randomized runs 50, the number of iterations 200 and stability criterion 0.00001. The significance of the outcome was determined by a Monte Carlo simulation for the suitable number of dimensions ($p < 0.05$). The final solution was obtained using three dimensions. We calculated the proportion of variance explained by each axis, i.e. the correlation between distance in the ordination space and distance in the original space. NMDS was conducted with PC-Ord ver. 5.10 (McCune & Grace 2002).

Indicator species analysis was used in order to identify the characteristic species for clearcut, young, mid-aged and old-growth stands (Dufrene & Legendre 1997). The randomness of indicator value distribution within species was tested using Monte Carlo simulation tests (4999 runs). Indicator species analysis was performed with PC-Ord ver. 5.10 (McCune & Grace 2002).

In order to measure differentiation diversity or spatial turnover in the species composition under homogeneous environmental conditions (also called beta diversity) within 10 × 10-m blocks, we used a metric advised by Colwell and Coddington (1994): the mean of the total number of unshared species between each pair of 1-m^2 plots divided by the number of species in the two plots combined, i.e. one minus the Jaccard coefficient of similarity (c.f. Harrison 1999, Chalcraft *et al*. 2004, Kluth & Bruelheide 2004). For each 10 × 10 m block, the Jaccard similarity index was calculated based on the data of five 1-m^2 plots.

The effect of successional age and soil parameters on the mean species richness of five 1-m^2 plots and on beta diversity was analysed using general regression model (GRM). The factors for the model were chosen with a backward stepwise procedure in order to find the optimal set of significant parameters. The following factors were used for the model: successional age (clearcut, young, mid-aged, old-growth), soil pH, organic matter, N, P, K, Ca and Mg contents. The analyses were performed with Statistica ver. 7.0 (StatSoft 2001).

Results

Species composition

In total, 99 species were identified: 57 species in old-growth stands, 54 species in mid-aged stands, 63 species in young stands and 81 species in clearcut areas. The most common species in all stands were *Oxalis acetosella*, *Rubus saxatilis*, *Luzula pilosa* and *Veronica chamaedrys*, which were identified in more than half of the plots within all age classes. About 20% of species were present only in the clearcut stands, e.g. *Viola canina*, *Potentilla erecta* and *Festuca pratensis*. Only two species (*Lathyrus sylvestris* and *Lysimachia nummularia*) were found exclusively in old-growth stands.

A three-dimensional NMDS solution provided a significant reduction in the variation ($p < 0.05$), while additional dimensions provided little further reduction. In total, the first three axes describe 81.1% of the total variance. The first axis accounted for 35.7%, the second 34.4% and the third 10.9% of the variance. There was a significant distinction between the species composition of different age classes (Fig. 1a). However, the blocks were not ordered according to the successional age — species composition in old-growth stands was more similar to the vegetation of young and clear-cut stands than to the composition of mid-aged stands. Soil pH and P content were correlated with the variance of species composition along the second axis. *Lycopodium annotinum*, *Pulmonaria obscura*, *Geum urbanum*, *Actaea spicata*, *Equisetum sylvaticum* and *Myosotis sylvatica* were prevalent in successionally older stands, whereas graminoids *Poa pratensis*, *Agrostis stolonifera*, *Elymus repens* and forbs *Epilobium angustifolium*, *Cirsium arvense* and *Scrophularia nodosa* were common in clear-cut areas or young stands (Fig. 1b).

According to indicator species analysis, only one species, *Galeobdolon luteum*, was characteristic of old-growth stands, and three species characterised mid-aged forest stands: *Maianthemum bifolium*, *Mycelis muralis* and *Actaea spicata* (Table 1). Clear-cut stands were characterised by 23 species. Among these species, grasses *Poa nemoralis*, *Agrostis capillaris*, *Deschampsia cespitosa* and forbs *Stellaria graminea*, *Epilo-*

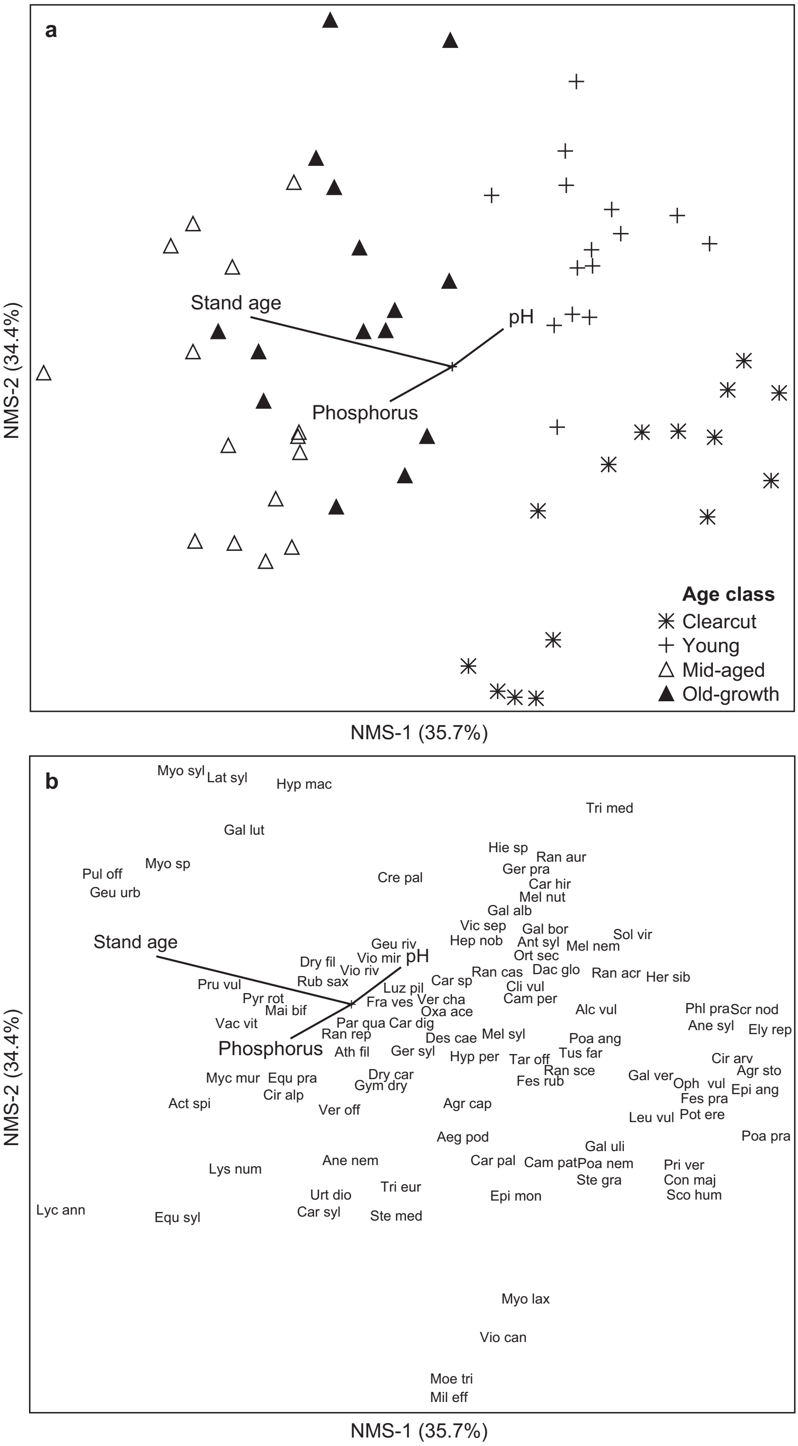

Fig. 1. NMDS ordination graph of 10 × 10-m blocks in forest stands of (**a**) different age classes and (**b**) species, and the position of environmental variables in relation to the first two axes ($r^2 \geq 0.15$).

bium montanum, *Campanula patula*, *Taraxacum officinale*, *Alchemilla vulgaris*, *Viola canina* and *Hypericum perforatum* had the highest indicator values. Young forest stands were characterised by *Dactylis glomerata*, *Anthriscus sylvestris*, *Hepatica nobilis*, *Melampyrum sylvestris*, *Galium album*, *Orthilia secunda*, *Crepis paludosa*, *Ranunculus auricomus* and *Melica nutans*.

Species diversity

The stepwise general regression model revealed that the species richness depended on successional age and Ca content. Species richness was significantly higher in clearcut and young stands than in mid-aged and old-growth stands ($F_{3,55} = 44.01$, $p < 0.001$; Fig. 2a) and was positively related to Ca content ($F_{1,55} = 9.52$, $p = 0.003$). The differentiation diversity was influenced by successional age: spatial turnover was significantly higher in clearcut and young stands than in mid-aged and old-growth stands ($F_{3,56} = 15.88$, $p < 0.001$; Fig. 2b).

Table 1. The list of species with a significant indicator value for clearcut, young, mid-aged or old-growth forest stands (column "Age class") according to the results of indicator species analysis. Frequency = species presence frequency in each age class.

Species	Age class	*p*	Indicator value	Frequency			
				Clearcut	Young	Mid-aged	Old-growth
Poa nemoralis	Clearcut	< 0.001	75	87	7	0	7
Stellaria graminea	Clearcut	< 0.001	74	80	7	0	0
Epilobium montanum	Clearcut	< 0.001	69	80	0	13	0
Campanula patula	Clearcut	< 0.001	51	67	13	0	7
Agrostis capillaris	Clearcut	< 0.001	43	87	40	40	7
Viola canina	Clearcut	< 0.001	40	40	0	0	0
Taraxacum officinale	Clearcut	0.002	46	80	40	7	13
Alchemilla vulgaris	Clearcut	0.002	42	67	33	0	7
Hypericum perforatum	Clearcut	0.003	39	100	73	40	40
Tussilago farfara	Clearcut	0.005	39	60	20	7	7
Galium uliginosum	Clearcut	0.005	34	40	0	0	7
Melampyrum nemorosum	Clearcut	0.006	37	67	40	0	13
Geranium sylvaticum	Clearcut	0.006	36	100	80	40	60
Epilobium angustifolium	Clearcut	0.007	27	27	0	0	0
Aegopodium podagraria	Clearcut	0.008	34	60	20	27	0
Deschampsia cespitosa	Clearcut	0.013	35	100	87	47	53
Myosotis laxa	Clearcut	0.015	27	27	0	0	0
Poa angustifolia	Clearcut	0.017	30	47	13	0	13
Trientalis europaea	Clearcut	0.020	30	47	7	13	7
Ranunculus acris	Clearcut	0.021	27	47	33	0	0
Veronica officinalis	Clearcut	0.026	30	67	7	47	27
Festuca pratensis	Clearcut	0.048	20	20	0	0	0
Potentilla erecta	Clearcut	0.048	20	20	0	0	0
Anthriscus sylvestris	Young	< 0.001	40	73	87	7	20
Hepatica nobilis	Young	0.002	39	73	100	7	73
Hieracium sp.	Young	0.003	36	0	47	0	13
Dactylis glomerata	Young	0.004	40	73	87	0	27
Ranunculus auricomus	Young	0.016	27	0	27	0	0
Orthilia secunda	Young	0.017	28	7	33	0	0
Galium album	Young	0.019	28	27	53	20	0
Melampyrum sylvaticum	Young	0.023	33	73	80	13	27
Melica nutans	Young	0.039	25	40	53	0	20
Crepis paludosa	Young	0.042	27	0	53	13	40
Maianthemum bifolium	Mid-aged	0.004	40	33	33	87	33
Mycelis muralis	Mid-aged	0.012	36	33	13	80	53
Actaea spicata	Mid-aged	0.041	24	0	0	33	13
Galeobdolon luteum	Old-growth	< 0.001	49	0	7	7	60

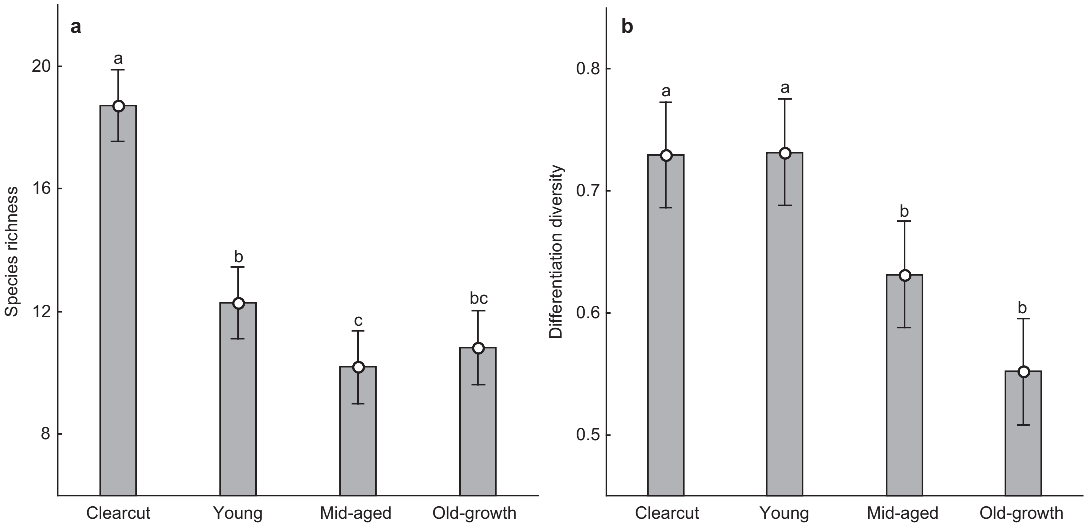

Fig. 2. Influence of forest stand successional age on (**a**) average species richness in five 1-m^2 plots, and (**b**) differentiation diversity (measured as one minus the Jaccard coefficient of similarity) of five 1-m^2 plots within 10 × 10-m plots. Letters denote homogeneity groups according to the Tukey-Kramer multiple comparison test.

Discussion

The results of this study showed that successional age was the main driver of understorey species composition in boreonemoral forests, while soil pH and P content accounted for some of the variation of community composition as well. Previous studies have indicated that differences in species composition and richness between young, intensively managed forests and old, less managed stands are relatively small (e.g. Graae & Heskjaer 1997, Okland *et al*. 2003). The greater differences between successional stages in our results may be attributed to the longer successional gradient covered in our study.

Species richness in 1-m^2 plots was higher in recently clearcut and young stands than in mid-aged and old stands, which is in accordance with the findings of earlier studies (Zobel 1989, 1993, Reich *et al*. 2001, Haeussler *et al*. 2002, Haeussler & Bergeron 2004, Small & McCarthy 2005). Although the proportion of characteristic forest plant species may decrease after clearcutting, other species may appear through germination from the soil seed bank (Zobel *et al*. 2007). Such species represent mostly ruderal strategy and remain in young forest communities, but wane gradually during the secondary succession. At the same time, clearcutting suppresses the abundance of species typical of old and mid-aged stands that may be caused by the following mechanisms: (i) competition with ruderals and inability to adapt to changed microhabitat; (ii) forest-floor herbs have slow growth and reproduction rates and therefore population densities recover slowly; (iii) many forest-floor species are clonal (e.g. *Oxalis acetosella*, *Hepatica nobilis*, *Galeobdolon luteum*), ant-dispersed (*Luzula pilosa*) or gravity-dispersed and are therefore slow occupants; (iv) temporal elimination for the gap-phase succession; (v) logging reduces the populations of rarer herbs (Meier *et al*. 1995).

The change in species composition during the successional phases is illustrated by the results of indicator species analysis according to which clearcut stands were characterized by light-demanding species typical of grassland communities like *Campanula patula*, *Agrostis capillaris*, *Melampyrum nemorosum* (Paal 1997) and well-known pioneer species common in clearcuts and other disturbed habitats, such as *Epilobium angustifolium* (Jantunen *et al*. 2001). Typical forest interior species like *Hepatica nobilis* and *Orthilia secunda* (Paal 1997) were common in young forest stands although some grassland species and species indicative of transitional habitats were still rather frequent as well, e.g. *Galium album* and *Ranunculus auricomus*. Interestingly, only a few species were characteristic to mid-aged stands and even less were confined to old-growth forest. This indicates that most of the typical forest species were still preserved in the understorey assemblages of clearcut and young stands though in comparatively lower frequencies than in successionally older stands. Therefore, none of these species was detected as an indicator of old-growth forest with the exception of *Galeobdolon luteum* that was very seldom present in successionally younger stands.

NMDS ordination showed, however, that the successional trend in species composition was not unidirectional because old stands resembled more early successional communities than mid-aged stands. The relatively higher similarity between young and old stands may be attributed to the gap structure of old-growth forests (Scheller & Mladenoff 2002), enabling the growth of some disturbance-related plant species.

The higher differentiation diversity in clearcut and young stands indicates that vegetation composition becomes more homogeneous during the secondary succession following clearcutting. This feature concurs with our previous comparison of young and old stands (Moora *et al.* 2007), but contradicts the common view according to which old-growth stands contain more heterogeneous vegetation (Qian *et al.* 1997, Bobiec 1998). Indeed, old-growth stands may be characterised by higher spatial variability of canopy structure (Fraver & White 2005), microtopography (Miller *et al.* 2002) and light conditions (Scheller & Mladenoff 2002). Evidence of spatial heterogeneity of understorey vegetation is, however, less decisive (e.g. Bobiec 1998, Scheller & Mladenoff 2002). Zobel *et al.* (1993) also studied the spatial variation of species richness in forest vegetation and recorded overdispersion of plant species diversity in recently clearcut areas and underdispersion in young forest stands. They concluded that it may be due to the patchy structure of recently disturbed vegetation caused by small-scale dispersal limitation.

One reason for the lower differentiation diversity in old stands might be the fine-grained structure of vegetation. Indeed, Scheller and Mladenoff (2002) found similar patch structure in old-growth versus mid-aged forest. Moora *et al.* (2009) showed that recently disturbed forest vegetation is characterised by a greater share of spatially less mobile rosette and hemirosette growth forms, whereas old stands display a greater share of vegetatively mobile erosulate growth forms. The ability of clonally mobile species to fill gaps between the less mobile plant individuals may result in homogenisation of vegetation composition in space, yielding less differentiation in diversity. Further studies are needed to show whether differentiation diversity may serve as a valuable indicator of the impact of forest management on understorey vegetation.

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